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COVER: *Epidendrum diforme* being visited by the moth **Amastas acona.**

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NATURAL POLLINATION OF ORCHIDS

C. H. DODSON AND G. P. FRYMIRE

THE pollination process of many plants is intensely interesting and none more so than in the case of orchids. One of Charles Darwin's most fascinating books dealt with pollination mechanisms in the orchids but unfortunately he was severely limited by a paucity of accurate information about pollination in tropical orchids. His comments were based upon deductions made from plants grown in the greenhouses of England and he had no opportunity to confirm them in the field. His work on the native orchids of Europe was based on actual observation and is excellent.

Paul Allen's works on the pollination of *Coryanthes, Gongora* and *Cycnoches* have been the only accurate observations of orchid pollination in the tropics of the western hemisphere since the time of Darwin. Unfortunately, due to pressure of other duties, Allen was unable to continue with this interesting subject.

We present here observations made in Ecuador on a number of tropical orchids which should give the reader an insight into the relationships between the flower and its pollinator. In most plants there is a high degree of dependency of one upon the other; however, in many of the highly evolved orchids it seems as if the orchid often takes complete advantage of the insect. The insect is not necessarily given reward in repayment for his visit and he is often trapped, flung about, burdened with heavy weights and even drugged as a consequence of his inquisitiveness. Such behavior on the part of the orchid has apparently come about as a response to an intrinsic need for maintenance of cross-pollination among its own kind while on the other hand barriers which discourage hybridization with other species are erected.

These observations point up the fact that much of the work of biologists is still to be performed out in the forests, deserts, mountains and lakes, in fact, anywhere in the open air. We are too often prone to think of the biologist in a white coat in a laboratory engrossed in study of a rack of test tubes or long-dead plant or animal specimens. There is yet, and will be for many centuries to come, a great deal of work to be done in direct contact with living organisms in their natural environment in an attempt to piece together the various and curious interrelationships of life.

In 1960, we initiated a series of

The Latin names of plants and insects are printed in the indicated type to assist the reader to quickly recognize them.

Orchid family—*Italics type.*

All other plant families—SMALL CAPITALS.

Insects (mostly bees)—**Bold face type.**

studies of pollination in tropical orchids in Ecuador and the following brief résumé of our field notes indicates the considerable success encountered. The photographs which accompany this article were, for the most part, made in the field. In some cases the original photographs were not satisfactory for reproduction and at a later time the same bees were reposed exactly as in the original photograph. Notation has been made in the subtitle of each picture which was reposed.

Observations

Our first observations of orchid pollination were made in December of 1959 on *Catasetum macroglossum* growing abundantly in the semi-arid regions on the coastal plain of Ecuador. These observations were particularly fascinating since we had read Darwin's account of the strange pollination mechanisms to be encountered here in the genus and were anxious to know whether his comments, which were made primarily on the basis of greenhouse studies supplemented by superficial observations by Dr. Cruger in Trinidad, were really valid. We did find the major portion dealing with the ability of these strange male flowers to fling pollinia onto the back of the unsuspecting bee, to be accurate. Surprisingly enough, the story goes far beyond Darwin's imagination. If Darwin had had the opportunity to actually see the flowers being visited by male bees only, to see the bees become intoxicated and fight among themselves for the right to enter a given flower, and to realize that the bees were not visiting the flowers for nectar or to gnaw the fleshy material inside but come as if drawn to the musky scent of the flowers to be drugged, he would surely have been even more impressed with the wonders of nature.

The male bee, **Eulaema cingulata**, hovering in front of a female flower of *Catasetum macroglossum*.

The first plant that we encountered with the bees actually visiting the flowers had female flowers (Fig. 4). The female flowers have a hood-shaped lip and the bees, attracted by the odor, would hover in front of the flowers for a few seconds and then land and crawl inside. We observed the bees scratching the inner surface of the flowers with the claws of their front tarsi,* "much as a dog digging a hole." After about 45 seconds of this behavior they would back out of the flower, hover in the air a few inches away from the flower and then repeat the process. Gradually the bees would become less wary and seemed to become intoxicated. Several bees were

*See glossary at the end of this paper for the meaning of such terms as tarsi, pollinia, metathorax, etc.

collected and forwarded to the Smithsonian Institution where they were determined by Dr. Carl Krombein as males of **Eulaema cingulata** and **E. tropica.** We also captured a female of similar morphology but of larger size and different coloration which we had seen entering a hollow limb of a large tree along a stream bed. This bee was determined as **E. dimidiata.** We observed several similar bees visiting flowers of PRESTONIA SP., a small flowered species of vine belonging to the Apocynaceae. This species of bee, however, was not attracted to the *Catasetum.*

Our next encounter with these bees was on Monticristi near Manta in the province of Manabi, on the 15th of January of 1960. The bees were observed visiting PRESTONIA MOLLIS and THEVETIA PERUVIANA, both of which are members of the Apocynaceae and are common in this region of dry desert. We did not actually see these bees accomplishing any pollination, but highly suspected them of pollinating *Trichocentrum tigrinum* var. *splendens,* an assumption which was later corroborated at the Instituto Botanico of the University of Guayaquil. Also working the Apocynaceous flowers were considerable numbers of **Eulaema tropica** and we captured one bee tentatively identified as **E. bomboides.** While on the hillside we noted that a high percentage of the flowers of *Oncidium hyphaematicum* were pollinated, and first suspected the **Eulaemas** of being the pollinators but though we placed flowers of PRESTONIA alongside the flowers of the *Oncidium* and the bees visited the PRESTONIA, they were not interested in the flowers of the fragrant *Oncidium.*

We did, however, observe a strange behavior pattern of a bee of the genus **Centris.** This bee (later found to be a male), about the same size as a worker honey bee, would sit on a stick near an erect inflorescence of the *Oncidium* and would drive away any other bee that passed nearby. Occasionally this bee would fly out and hover in front of the inflorescence of the *Oncidium* and when the wind moved the inflorescence the bee would dart in and strike a flower. The bees of this genus are extremely rapid fliers. Investigation showed the flowers to be freshly pollinated after the bee had

Male flowers of *Catasetum macroglossum* with three species of **Eulaema, E. cingulata, E. tropica** and **E. bomboides,** visiting. (posed)

struck them. After we removed the flower spike the bee left but we discovered him shortly thereafter near another spike of *Oncidium* flowers continuing the same behavior. Near this *Oncidium* inflorescence was an inflorescence of PRESTONIA MOLLIS which was regularly visited by **Eulaema.** The bee was extremely busy chasing other bees and we later captured him by employing a "double envelopment" by simultaneously swinging our insect nets from opposite directions.

From here we moved to Quevedo and found a plant of *Stanhopea tricornis* in the cacao trees nearby. We took it to town overnight for safekeeping. The buds opened on it the following morning. We took it back out to the cacao orchard, gathered several specimens of the various species of orchids in flower in the area and made a "set-up." By concentrating a number of orchids in flower in one locale we felt that the possibility for attraction of the pollinator would be enhanced. At about 9 A. M. two male bees of **Eulaema dimidiata** visited the flowers and were photographed. The bees searched for some time to find the entrance to the flowers but finally got in and upon leaving picked up the pollinia on their dorsal metathorax. Nests of what later proved to be **Euplusia smaragdina** were observed on the ceiling of a store along the road.

Our next trip was to Bucay, on the railroad from Guayaquil to Quito. During the first few days of February it rained regularly. Along the railroad near the edge of town a plant of *Epidendrum difforme* was found growing on a fence post. The flowers were examined and the pollinia matched perfectly those found on a moth, **Amastus acona,** on the road from Duran to Tambo during the previous week. The length of the nectary of the flower matched perfectly the location of the pollinia on the proboscis of the moth. We found only one other *Epidendrum* which was in flower in this region, and its pollinia were very different from those of *Epidendrum difforme.* In the morning we took the train down to La Lolita, west of Bucay, at 350 meters elevation, to observe nests of **Euplusia smaragdina** which we had noted in the walls of the railroad station. We arrived

Male bee of the genus **Centris,** hovering in front of the flower of *Oncidium hyphaematicum,* with pollinia attached to its head from a previous flower. (posed)

The bee striking the flower and leaving pollinia in the stigma. (posed)

Drawing showing the steps by which pollination occurs in *Stanhopea tricornis*

before dawn, in the rain, and observed the bees leaving the nests at the first sign of light. The bees came and went, for the rest of the day, carrying food and bark for nest construction. One female bee was captured with pollinia of *Sobralia violacea* on her dorsal thorax. No male bees were observed in the area. The nests consisted of numerous cells constructed of bark held together with liquid which we believe to be sap which the bees were observed collecting from SPONDIAS MOMBIN (Anacardiaceae). The cells make up tubes up to 15 cm. long and 1 cm. in diameter. Each tube is a series of cells constructed parallel, when space is available. As soon as it is long enough, a sweet sugar-like material is placed inside to a depth of about 8 mm., an egg is laid and the cell is sealed off leaving a cavity about 2.5 cm. long. Work continues extending the same cell. Apparently only one female works on each tube but other females often build a tube alongside, forming a colony. Perhaps 20 females were working at this site. In one of the termite-eaten beams inside the building we found nests of **Euglossa viridissima** and several female bees of this species were collected while coming to the nest. They had a base color of metallic green but varied considerably in color, some having a golden or bronze cast. Several male bees were captured outside of the building where they were hovering

around some of the plants. Also collected here were several kinds of small and large carpenter bees working in the beams, as well as some small **Centris** which had nests in small holes.

The following day we caught the train up to Olimpo, elev. 900 meters. In back of the station are some thorn forests near the small branch of the river Chanchan. Many plants of *Catasetum macroglossum* occur here and **Eulaema tropica, E. bomboides, E. cingulata** and **E. speciosa** were captured working the *Catasetum*. Some of the bees had as many as three pollinaria of *Catasetum* attached to their dorsal thorax. Some had pollinia of *Sobralia violacea* and in one case, first *Catasetum* then *Sobralia* and then *Catasetum* pollinaria were superimposed. The bees enter the male *Catasetum* flowers in the same manner as the female flowers but encounter the antennae of the male flowers which, when touched, cause the viscid disk of the pollinarium to be flung upward and strike the dorsal thorax of the bee, immediately becoming cemented into place. The male bees reacted in the same manner as in the first observation and fought with each other for the opportunity to enter the flowers.

Also growing here are *Lycaste xytriophora,* which we observed being visited by **Euglossa viridissima,** and *Stanhopea bucephalus,* which was visited by **Eulaema bomboides.** The *Lycaste* is pollinated in rather a simple manner, the bee entering the rather large flower by landing on the outstretched lip and having the pollinarium stuck to the underside of the dorsal projection of the metathorax when he backs out. In repeating the process at another flower the bee leaves the pollinia in the stigma upon backing out. Pollination of the *Stanhopea* is much more complex. In this species the bees fly into the space between the lip and the column and, being unable to hold on to the slippery surfaces, fall down and through the flower, picking up the pollinia on the underside of the dorsal projection of the metathorax on their way through. The flowers cannot be pollinated immediately thereafter due to the stigma being closed. The stigma does not open until the following day, thereby making cross-pollination nearly obligate.

Only in the case of the *Sobralia* is food, that can be ingested with the ligual processes of the bees, provided by the flower and in that case both male and female bees are attracted. In the other cases, i.e., *Catasetum, Lycaste* and the two *Stanhopeas,* no apparent food of any kind was available nor did the bees attempt to chew the fleshy parts of the flowers. This same pattern was found to hold through all of our observations.

Over a period of a year we had brought a considerable number of orchids in to the garden at the Instituto Botanico at Guayaquil and numerous bees of **Eulaema cingulata, E. tropica** and **Euplusia smaragdina** were present in the garden and did often visit these flowers. **Euglossa viridissima** was also present and visited and pollinated *Trichopilia rostrata.* This is a relatively simple flower as is *Lycaste xytriophora.* In this case, however, the pollinarium is attached to the frons of the bee rather than the

metathorax when the bee forces his way into the tubular flower. The stipe of the pollinarium depresses due to differential drying and when the bee enters the next flower, the pollinia are in such a position as to be forced into the stigma of the flower.

Males of **Euplusia** were observed visiting HIBISCUS flowers and were commonly found visiting THEVETIA PERUVIANA from January to May, but when the evenings became cool in mid-May the bees no longer came. Females of **E. smaragdina** were observed in abundance at THEVETIA but did not visit the HIBISCUS. Bees were marked in January and were observed until May indicating that both male and female bees are long-lived. **Eulaema tropica** visited two species of ANTHURIUM on several occasions. Males and females of **Euplusia smaragdina, Eulaema tropica** and **Xylocopa frontinalis** visited and pollinated *Sobralia violacea* in the garden.

We had brought the beam which contained the nests of **Euglossa viridissima** back to the Institute and a female bee which had apparently hatched from one of the cells was found trapped in a hybrid *Cattleya*. She had become tangled in the stigmatic area of the flower. The nests of the **Euglossas** are constructed of a waxy material which is soft at first but later takes on a hardness like shellac. The cells are individual and not necessarily joined together but the whole cavity containing the cells was coated with the same wax, indicating a community effort.

Euglossas were noted visiting THEVETIA PERUVIANA, IMPATIENS BALSAMINA and several members of the Bignoniaceae.

Males of **Euplusia smaragdina** were observed pollinating *Notylia wullschlaegeliana*, plants of which had been brought into the garden from Monticristi. The bee would land on the capitate cluster of small pink flowers, grasp a flower and thrust its head into the front of the flower thereby having the viscidium of the pollinia stuck to the frons of the bee. The stipe depresses and the pollinia are then deposited in the narrow stigma on the front of the column. The flowers can not normally be self-pollinated for the stigma does not open for several hours after the pollinia have been removed.

Two male specimens of **Euplusia smaragdina** were collected, which had pollinaria of an unidentified orchid on the trochanters and femurs of the second pair of legs. The viscidium was curved around the front side of the leg, the long slender stipe extended to the rear 3.5 mm. and then turned 180° for 4 mm., placing the pollinia in front and slightly below the leg. No orchid has been found to match these pollinia. We discovered a new genus of orchid allied to *Notylia* near Loja in southern Ecuador and the pollinarium of this orchid is very similar to that found on the bee. This might suggest that another species of this new genus of orchid will eventually be found in the region of Guayaquil. The bees were collected from THEVETIA PERUVIANA in April.

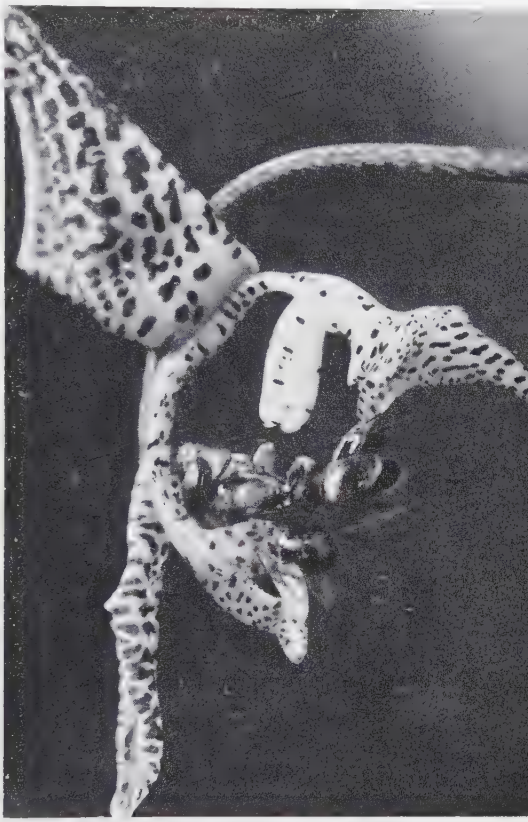
A short, half-day, trip was made in late March to La Toma, north of

Guayaquil on the road to Quevedo. Here numerous plants of *Oncidium pardothyrsus* were in flower and a small **Centris** was observed pollinating one of these plants following the same behavior pattern noted in the pollination of *O. hyphaematicum* by the **Centris** at Monticristi. The bee would hover in front of the flowers and the pendant racemes and when the wind moved them, would fly in and strike one of the flowers. The plant was collected and nearly all of the 20 flowers had been freshly pollinated. We kept the plant and later noted that all but one of the seed pods dropped off, indicating that the plants are self-incompatible and that only the first pollinia, brought by the bee from another plant, was effective in fertilization of the flower.

The next major trip was made in early April to Quevedo. Several species of orchids were in flower here and a number of flowering plants were collected and a "set-up" was made. Great quantities of *Aspasia epidendroides* were in flower and were observed being pollinated by males and females of **Eulaema cingulata** and **E. tropica.** This orchid has a long column which extends beyond the down-curved lip. It also has a relatively deep nectary contained in the space where the lip is adnate to the column. The lip is white and the rest of the flower is yellow-white with brown bars. The flowers have a strong clove oil odor. The bees hover in front of a particular flower and lower their long proboscis to a semi-forward projecting position before landing. Usually only one or two of the 6 or 8 flowers are ready at a given time and the bees apparently sense this by odor being stronger when the flowers are ripe. Upon landing, the proboscis is inserted into the nectar tube and the bee grasps the lip and hangs on. The bee's head is in position so that in drinking the nectar his frons touches the sticky viscidium and the pollinarium is carried away, cemented to his frons, when he leaves. The stipe depresses and upon visiting the next flower the pollinia are pushed into the sticky stigma and are pulled from the bee's head when he again leaves.

Plants of *Gongora maculata* were in flower in abundance and numerous male bees of **Euglossa viridissima** and a dark blue-purple species of **Euglossa** were observed pollinating them. The flowers have a strong musky odor suggestive of dead fish. Our observations corroborated those published by Paul Allen in that the bee lands on the inverted fleshy lip and once again scratches with the front tarsi on the inner portion of the hypochile. The bee does not stay in this position for long and in attempting to regain flight, falls downward, sliding on the curved surface of the column until it hits the protruding viscidium. The viscidium and rostellum slide under its thorax and the sticky viscidium is cemented in place. The same procedure pollinates the flower but only in flowers which are a day older and have the narrow stigmatic pocket open and receptive. The bees do not give up after the first few tries but persistently continue to work the inflorescence for hours. These plants are closely related to *Stanhopea* and in many of

Euglossa viridissima scratching the lip of *Gongora maculata*. (posed)



The bee sliding down the column and contacting the rostellum of the flower where the viscidium of the pollinarium is stuck under his metathorax. (posed)

these orchids the flowers last only a day or two after opening. This phenomenon is apparently caused by the flowers not opening until they are completely mature. In *Gongora* and *Stanhopea* most of the flowers on an inflorescence are open within a matter of a few minutes after the first flower opens. In most orchids the flowers open gradually and only a few flowers are completely mature at a given time. Many of these will ultimately have all of their flowers mature at the same time but often considerable time passes before this is so.

Cycnoches lehmannii was in flower in quantity during this season and only male **Eulaema cingulata** were observed to visit these flowers. The other species of **Eulaema** were present but did not visit this species even though other orchids which they did visit were in close proximity. The very strong odor emitted by this orchid is similar in many respects to that of *Catasetum macroglossum* but has subtle differences which are easily noted even by the human nose. Certainly the bees

differentiate without difficulty for though **E. cingulata** visits both orchids indiscriminately the other species of **Eulaema** are not attracted to *Cycnoches* as we demonstrated in the garden of the Instituto on numerous occasions. The bees fly to the male flowers of this species and land on the inverted lip, clutching the claw of the lip with the 2nd and 3rd pair of legs and scratching the surface of the lip just beyond the callus with the claws of the tarsi of the first pair of legs. As in *Catasetum* and many of the other orchids of the *Stanhopeinae* and *Catasetinae* the male bees of the **Euglossini** seem to take on an intoxicated behavior from scratching the lips of the flowers and sopping up the exuded liquid from the epidermal cells with chemo-receptive pads present on the tarsi of these bees. These pads do not occur on the tarsi of the female bees. The callus of the lip in the *Cycnoches* extends out so far that the bee must release its grip with its 3rd pair of legs and swing the abdomen down to reach the source of the odor with the 1st pair of legs. In doing so the abdomen touches the tip of the column of the flower and by only very slightly lifting the anther-cover on the tip of the column, releases the tension-bound stipe of the pollinarium which whips up carrying the sticky viscidium causing it to strike the bee on the terminal ventral surface of the abdomen. The viscidium is cemented tightly to the bee's body and the stipe is curled tightly. The anther cap remains over the pollinia for at least half an hour, the stipe gradually dries and straightens out leaving the pollinia extended straight out in back of the bee.

The bee then flies on and encounters the female flowers which in this species are rather similar in form to the male flowers but are larger and have a short fleshy column rather than a long slender column. The same procedure occurs again but in this case the apex of the column of the flower has 3 hooks spaced so that when the round pollinia pass between one pair of them there is not sufficient space for them to pass through and one pollen mass is pulled off. The stigma is just below the hooks and the pollinia are forced into the stigmatic juices.

The female flowers occur only on robust plants which have been in full sunlight during the growing season. Less robust plants and plants which have been in partial shade during the growing season normally produce only male flowers. About 25 male inflorescences are produced for each female in the population and the male flowers last only 3–5 days while the female flowers last from 6 weeks to 2 months.

The same pollination phenomena were reported by Paul Allen in *Cycnoches ventricosum* in Costa Rica, in his revision of the genus. The same pollinator, **E. cingulata,** was reported for this Central American species also.

A species of MARANTA (Marantaceae) with heads of yellow flowers was abundant in this region and the bees were observed visiting these flowers to secure food. The bees would hover in front of the flowers, lower the tongue and insert it into the tubular flower in the same act as landing. Both males and females of **Eulaema**

cingulata, E. tropica and **Euplusia smaragdina** were collected from these flowers. Also **Exaerete smaragdina,** a large parasitic bee, which is parasitic on the nests of **Euplusia smaragdina,** of a brilliant metallic green color, was captured from these flowers and both males and females were taken.

More plants of *Stanhopea tricornis* were found in flower and placed in the set-up. Once again they were visited by **Eulaema dimidiata** as mentioned previously. The other species of **Eulaema** showed no interest in this *Stanhopea.*

Two bees which were captured on *Gongora maculata* had foreign pollinaria on their backs. One of these pollinaria, on the metathorax of a male **Euglossa viridissima,** was later determined to be from a *Cyrtopodium,* probably *C. punctatum.* The other, on the abdomen of the same species of bee, was from some type of *Zygopetalum* ally, probably a *Chondrorhyncha* or *Pescatoria.*

Male bees of **E. tropica** visited *Pescatoria wallisii* in the set-up. These flowers are rather open and simple and the bee simply forces his way in between the lip and column and the pollinarium of the flower is deposited on the terminal extension of the metathorax. These flowers have a sickeningly sweet fragrance.

In the latter part of April a trip was made to Balzapamba in the Province of Bolivar on the road from Babahoyo to Guaranda. Balzapamba is at an elevation of 775 meters and is on the western slopes of the Andes in the cloud forest region. An enormous number of orchid species are to be found in this region. We collected several species and made a set-up. *Gongora maculata* was abundant and we collected a number of **Euglossa viridissima** and the blue-purple species of **Euglossa** working these flowers. The only species of **Eulaema** encountered here was **E. cingulata,** but we found a large nest of this species located in an embankment near the bank of the river. The embankment apparently consisted of an old stream bed containing loosely piled stones which were later covered by soil. This left numerous holes and spaces in which all manner of animals make their homes. Approximately 25 female bees were observed coming and going at the nest, entering by way of a small hole in the dirt covering the embankment. The bees were noted carrying nesting material on the tibias of the 3rd pair of legs. They also brought in a white material, carried in the same manner, apparently for use as food for the young developing bees in the cells. An excavation was made

Eulaema tropica visiting and pollinating *Pescatoria wallisii.*

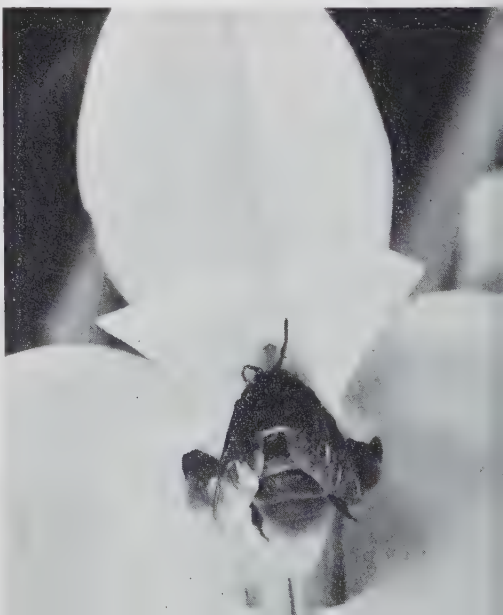
by removing the stones so that the nest could be observed. It was located approximately one meter inside of the embankment and was about one foot in diameter. A large accumulation of cells were in the nest, most of them old and discarded. The cells are constructed side by side in a loose order, each cell being about an inch long and oval in outline; the cell is constructed of fecal matter and the lower one-third is filled with the sweet white material. Then an egg is laid and the top of the urn-like cell is sealed over with a thinner cap of the same fecal matter. Many of the cells were parasitized.

This nest was apparently rather old and quite large. Six definite stages in construction were evident, with the first consisting of some 10 nearly decomposed cells. The second of about 25 was less decomposed. The third was of about 75, the fourth of about 125. The fifth had about the same number of which most were unhatched. The sixth was in construction and had some 20 cells sealed and 5 still open. Some of the cells of the fifth stage were opened and found to contain female bees in various stages of development, some ready to hatch. The sixth was removed and taken back to the Instituto and was later sent to the Missouri Botanical Garden. The bees hatched and all proved to be male bees. They hatched in mid-August, making a total elapsed time from collection and construction to hatching of about 4 months. The bees hatched over a period of about one week.

While we were excavating, the bees continued to work the nest, not at all disturbed by our presence. When the nest was finally open, a lone female bee appeared to be guarding the nest. She would come to the front of the nest each time the cells were disturbed and would make a fierce buzzing noise for a few seconds and then would return to the back of the nest. She refused to be driven away until some of the cells were removed. She appeared to be a young bee without the duller color of the older, shopworn females. One bee which was captured from the nest had brown hair covering the thorax rather than the typical black of the other females.

One female was captured with the pollinia of *Maxillaria grandiflora* affixed to the terminal projection of the metathorax. *Maxillaria grandiflora* was found in flower further up the road at an elevation of 1400 meters. This orchid produces a quantity of globular cells in the basal cavity of the lip which are apparently eaten by the bees.

Female bee of **Eulaema cingulata** visiting and pollinating *Maxillaria grandiflora*. (posed)



The color of the flower is white with a yellow and red lip. The lip is concave and the side-lobes surround the column until the bee forces the lip open. The flower is fragrant with a musty-sweet odor.

Two strange beetles were found which were parasitizing the cells, apparently eating the sweet food that the bees were placing in the open cells. The beetles were in an immature stage, were completely without visible eyes and had a morphological form very similar to that of the **Eulaemas** in that they had similar antennae, head shape, legs and bodies. The legs even had spines similar to those on the inside of the tibia of the bees. These beetle parasites have been reported for other bees and apparently the female beetles lay their sticky eggs in such a way that they are carried to flowers by the bee, left there, and picked up on the bodies of other visiting bees who then carry them to their nests.

Further up the road east of Balzapamba at an elevation of 1300 meters a large population of *Bletia purpurea* is found along the road cuts. Several bees were observed pollinating these small pink flowers. Abundant nectar is produced by these flowers in the nectary at the base of the lip. **Euglossa viridissima** and two undetermined species of bees were captured while visiting these flowers. All had pollinia of this *Bletia* on their dorsal thorax. Further up the road at 1400 meters elevation, a new species of *Catasetum*, which has not yet been named, was observed being pollinated by **E. cingulata.** This *Catasetum* has a strong odor of clove oil, similar to

Eulaema cingulata visiting *Catasetum fragrans* and receiving the pollinia on the underside of the thorax. (posed)

that of *Aspasia epidendroides.* The plants grow as terrestrials on very steep slopes. The flowers of this species are quite different from most *Catasetums* in that the flowers are perfect and the fleshy, short column is adnate to the fleshy, concave lip. The flowers are considerably smaller than the average *Catasetum.* The bee does not actually enter the flower but rather lands on the surface of the flower with its thorax over the column and its head entering the cavity of the lip. The pollinarium in this species is organized very similarly to that of *Cycnoches* and requires only a slight movement of the anther cap to be discharged. Males of **Eulaema cingulata** pollinate this species and the

pollinaria are stuck to the ventral portion of the thorax either in front of or between the legs. The pollinia are extended more or less at right angles on the end of the stipe. The stigma is in a cavity with sloping sides, leaving a hole, broad in the center but narrow at the sides. When the bee lands on another flower the pollinia which are extended down from the bee's thorax are pushed into the sloping cavity and are compressed so as to enter the cavity. Once inside, the pollinia again separate and are trapped by the narrower margins of the cavity. When the bees pull away, the pollinia are pulled off and pollination is completed.

Along the road cuts in this area are abundant plants of *Epidendrum ibaguense*. These were observed being pollinated by a swallow-tailed skipper which landed on top of the cluster of flowers and inserted its long proboscis into each of the erect, non-resupinate flowers. The pollinia stick to the skipper's proboscis and are carried from one flower to another.

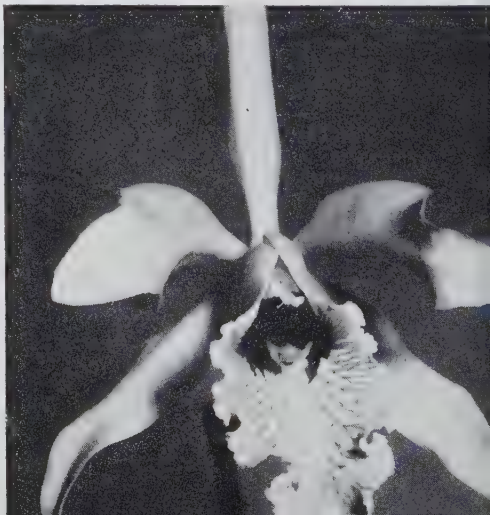
In passing through Babahoyo on our way home we noted that great quantities of nests of **Euplusia smaragdina** are stuck to the ceilings of the buildings where they are built over the sidewalks. Large clusters of cells were common.

Back at the Instituto Botanico a curious situation was observed. A large plant of *Oncidium onustum* which had been brought in and planted in a tree, produced 7 or 8 large inflorescences. For the first few weeks none of the flowers were pollinated, but one day it was noticed that some of the flowers had been visited and pollinated. This continued for several days in succession and finally a female bee of **Xylocopa frontinalis** was observed visiting these flowers. The bee was captured and had pollinaria of this *Oncidium* on its frons. After the capture of this bee, pollination of the flowers ceased for about 3 weeks and then once again commenced. Another **Xylocopa** of the same species and sex was captured.

It appears as though these bees can learn to visit such flowers. During this entire period considerable quantities of male and female **Xylocopa frontinalis** were present at all times in the garden visiting roses, ginger, Hibiscus and *Sobralia* as well as various Legumes. Only the two bees ever learned to visit the *Oncidium*. They were apparently attracted by the odor for they did not pause for more than a moment on any given flower. The fragrance of the flowers is sweet with a tang of orange blossoms.

The month of May was spent in Guayaquil with a few short trips north of the city where a number of **Eu-**

Eulaema tropica visiting *Cattleya maxima*. (posed)



laema cingulata, E. tropica, E. dimidiata and **Euglossa viridissima** were collected while visiting PRESTONIA MOLLIS, several Legumes and Bignons. Also several **Centris** were collected, from a Malpighiaceous vine, which were quite similar to the bee which visited *Oncidium hyphaematicum* on Monticristi. A week-end trip was made in early June to Manglaralto on the beach, north of Salinas. A large number of **Eulaema tropica** were collected from THEVETIA PERUVIANA. It was hoped that we would be able to confirm our prior observations at the Instituto Botanico that this species of bee pollinates *Cattleya maxima,* but the *Cattleya* was not in flower during this season. We had previously found pollinia of *C. maxima* on a flower of *Sobralia violacea* which had been visited by **E. tropica** in the garden at the Instituto.

In July, a trip was made to Loja in southern Ecuador and on over into the Amazon headwaters on the eastern side of the Andes. This region is one of the richest for orchid flora in the world. From the pass on the road from Loja to Zamora, at an elevation of 2800 meters the mountains decrease in altitude to 1000 meters at Zamora, a small town east of Loja. The climate is always cold and misty at the pass and becomes warmer gradually and more sunny warm days occur as the elevation decreases. The forested slopes maintain a great quantity of orchid species stratified according to their ecological needs. At Zamora a large number of **Eulaemas** were observed visiting the flowers of INGA SP. (Leguminosae) and a few **Eulaema cingulata** were collected from BIXA ORELLANA (Bixaceae). An extensive population of *Stanhopea wardii* occurs from km. 45 to many kms. below Zamora. The population is quite variable throughout but shows a cline from the upper end down to Zamora. From that point on out to Yansasa the cline is no longer evident and the variation appears to be at random. The presence of this cline from Zamora appears to be attributable to the fact that the pollinating **Eulaemas** apparently do not make their nests at elevations much higher than that of Zamora (1000 m.). These bees do range for long distances up the canyons during the occasional sunny warm days. The flowers of the *Stanhopeas* which occur at the higher elevations are much more fleshy and last considerably longer than do the flowers at the lower elevations. This may well be due to the need for a longer waiting period for pollination. The color seems to be correlated with fleshiness. The more fleshy flowers are much more yellow and the fleshiest are completely orange-yellow.

The pollinator of these *Stanhopea* flowers was not actually observed but it was suspected that it must be a species of **Eulaema** observed in abundance in this area. This species might be **E. niveofasciata,** very similar to **E. bomboides,** differing only in color. The abdomen in this species is barred with black and white stripes on the upper two-thirds and is copper-red for the lower one-third. Set-ups were made to attract these bees using female *Catasetum* flowers but none of them were attracted. Several **Eulaema**

cingulata did come however but did not demonstrate any interest in the *Stanhopea* flowers. We concluded from this that **E. cingulata** definitely does not pollinate *Stanhopea wardii* in this region and that, quite possibly, **E. niveofasciata** is the pollinator.

Elleanthus capitatus, representative of a genus closely allied to *Sobralia,* was flowering abundantly. The large plants with canes up to 6 feet long are pendant from large limbs of trees overhanging the river. The inflorescence is capitate and reminds one somewhat of a compound flower such as found in the Compositae. The purple flowers are small (¼ of an inch in diameter) and the buds are sunken in a mass of gelatin-like material. When the flowers are mature they protrude slightly from the gelatinous mass. These plants were also placed in a set-up but during many hours of observation nothing was seen to visit them. Later while traveling down the river by canoe, where we were passing under the trees regularly, we observed the flowers being visited by humming birds. The birds would spend several minutes hovering under each inflorescence, moving from flower to flower.

On the river trip to Yansasa, a tiny pueblo at 800 meters elevation, northeast of Zamora, along the Rio Zamora, pollination of *Cycnoches egertonianum* was observed. This species is representative of the heteromorphic group of *Cycnoches* in which the female flowers are morphologically very similar to those of the *Eucycnoches* group represented in Ecuador by *C. lehmannii*; however, they are somewhat smaller. The difference between the two groups of *Cycnoches* is dramatically demon-

Eulaema cingulata swinging free from lip of the male flower of *Cycnoches lehmanii,* touching and discharging the pollinia and receiving the pollinia on the apex of the abdomen.

The bee swinging free from the male flower of *Cycnoches lehmanii* just before depositing the pollinia in the stigma. (posed)

Euglossa viridissima landing on the flexible lip of the male flower of *Cycnoches egertonianum* and touching the anther cap which causes the pollinia to be thrown and be attached to the abdomen of the bee.

The same bee visiting the female flower and leaving the pollinia in the stigma.

strated by the male flowers of *Cycnoches egertonianum*. These flowers are much smaller than the others, are carried in long multiflowered, pendant spikes, and rather than having an entire blade to the lip, have a multipronged, divided blade. The claw of the lip in this species is flexible rather than being stiff and erect as in *C. lehmannii*.

Cycnoches egertonianum is pollinated by the small **Euglossa viridissima** males. *Cycnoches lehmannii* and *C. ventricosum* are pollinated by **Eulaema cingulata** as mentioned previously. The bees land on the pronged apex of the lip and the weight of the bee causes the claw of the lip to bend down, permitting the end of the abdomen of the bee to touch the anther cap on the tip of the elongated column. When the anther cap is disturbed, the pollinarium is released and flies up, the sticky viscidium striking and sticking to the bee's abdomen just as in the other species of *Cycnoches*. The pollination of the female flowers is precisely similar to the pollination of other species of *Cycnoches*. The column has the same three prongs which act to strip the pollinia from the abdomen of the bee as he falls past, attempting to orient himself after dropping away from the lip.

After our return to Guayaquil we made several trips to an area northwest of Guayaquil on the road to Salinas. These trips were only for a few hours each but a number of **Eulaema** were collected here. A stream comes down from the mountains above the Hacienda Cerro-Azul, forming a densely wooded arroyo. A few hundred yards above the cement plant the stream bed is about 10 yards wide, the walls rising rather abruptly. A few

large trees with rough scaly bark grow in the stream bed. These trees exude a white latex when damaged or wounded and the **Eulaema** come to these trees and drink the exuding sap.

A collection of 17 bees was made here. Two were male **Eulaema bomboides,** one was **E. cingulata** female. The rest consisted of an extremely variable population of **E. dimidiata.** Thirteen were males and one was female. The 13 males varied considerably in color but not in form. The color varied in several respects. The base color varied from metallic-green to blue-green to dark blue. The hair color varied from bees with bands of yellow and black to others which were yellow and black for the upper two-thirds of the abdomen and copper-red for the lower one-third; others were black with white bands and were copper-red for the lower one-third.

Conclusions

We have attempted for the most part to limit the above résumé to what we actually observed and to keep our evaluation of those observations to a minimum. This is not always possible and there is always a great deal of pressure to try to interpret those observations in relation to observations of other pollination phenomena reported by other investigators. The following then, is a brief summary of some of the observations in the light of what is known of such phenomena at the present time.

It appears as though we have been given the opportunity to lift the edge of the canvas covering the picture of the intricate mechanisms for their pollination which have been developed by certain of the advanced orchids. This peek at the picture left us with far more questions than answers. We saw only certain parts of the picture. Whole areas, which from the strange morphological characteristics of the flowers, promise to be fascinating, were not seen. A great many observations need to be accumulated before the rest of the picture will begin to become clear.

Certain of the observations present phenomena new to floral ecology—others tend to clarify and confirm previous reports such as the presence of flowers which attract only male bees.

The phenomenon of the **Centris** striking and thereby pollinating the *Oncidium* is new to floral ecology. There are two major possibilities for explanation of this behavior. Both involve the question of what the bee sees. First, it may be a case of pseudocopulation in which the bee sees the flower as a desirable female. This has been reported in other orchids but may not be applicable here. The bee strikes the flower and returns to its position hovering nearby so rapidly that the whole process can be missed in the blinking of an eye. The bee makes no attempt to land. Second, the behavior may be attributable to territorial protection. This has been reported for male **Bombus** in which the bee sits on a stick in the middle of a garden and drives away all other insects which enter the garden. The **Centris** appeared to be reacting in this way and industriously attacked any flying insect which passed through his territory. If this is true, then the bee must see the moving *Oncidium* flowers as flying

insects and strike them in an attempt to drive them away. The flowers are produced on long arching racemes which are swayed by the slightest breeze. This movement may appear to the bee as a flying insect. Or, the bee may see the flowers as something entirely different from what we see. It has been reported many times that bees see a different spectrum than do humans and particularly in the ultraviolet ranges. Perhaps the flower actually looks like another insect to an insect.

The importance of the observations of the pollination of the two types of *Cycnoches* lies in the discovery that the two groups of *Cycnoches* are not only morphologically different but are also ecologically different in the sense that different types of pollinators are required. The inference is, of course, that the reason the heteromorphic types of *Cycnoches* are distinct from the *Eucycnoches* group is centered on the evolution of a mechanical pollination system based on separate morphological characteristics of the pollinators available. The difference is apparently based on development of separate means of attraction of these two different types of insects. That the two types of insects are not really far separated in relationship to one another is certainly significant. The presence of a group of closely allied but morphologically distinct insects with slightly different behavior patterns, has permitted the evolution of a distinct group of plants.

There is considerable evidence that many of the remarkably unique orchids of the Western Hemisphere have had their development based on similar phenomena. Many of these orchids use male bees of the tribe **Euglossini**—either the genera **Eulaema, Euplusia** or **Euglossa**—as their pollinators. It seems that these bees are particularly susceptible to being attracted to flowers which do not provide food that the bee can use for sustenance. It is interesting to note that the female bees are not attracted to this type of flower. Perhaps the female bee cannot sense the presence of such flowers. One of the obvious differences between the male and female bees is the presence of chemoreceptive pads on the tarsi of the front pair of legs of the male bee. These pads may enable the male bee to sense the odors of these flowers. The reaction of the male bees to these flowers indicates that the senses of the bee are dulled and the bee becomes "intoxicated." In such a condition, the bee becomes susceptible to manipulation in unique manners to accomplish pollination.

No orchids with these types of floral mechanisms are to be found outside of the western hemisphere nor are the **Euglossini** encountered outside of the same area. It appears as though the orchids of these groups which "deceive and manipulate" the male bees have developed in this hemisphere in response to the presence of bees with a peculiar social organization, morphological characteristics and behavior patterns. For the most part, orchids which have distribution patterns which cover both hemispheres use insects which are present in both hemispheres as pollinators. In other instances, or-

chids which are limited to one hemisphere have counterparts in the other and are pollinated by similar insects. Many of the tropical American orchids such as true *Epidendrum*, *Spiranthes* and its allied genera, *Habenaria* and the Sarcanthine orchids, are probably pollinated by Lepidoptera in a similar manner to the Sarcanthine orchids and other Lepidoptera-pollinated orchids which form a major portion of the orchid flora of the eastern hemisphere. Another large group of orchids, the *Bulbophyllum* and its allies, in the eastern hemisphere are fly pollinated. It seems probable that many of the *Pleurothallids* in the western hemisphere form a parallel situation and are fly pollinated. The large, open-flowered orchids of the eastern hemisphere such as *Grammatophyllum*, *Cymbidium* and *Vanda* are pollinated for the most part by **Xylocopa.** These are rather simple in structure and compare quite well with orchids in the western hemisphere such as *Zygopetalum*, *Lycaste*, *Maxillaria* and their allies which appear to be pollinated by **Euglossini** instead of **Xylocopa.**

Another large class of orchids which either occur in both hemispheres or have similar counterparts in both hemispheres appear to be promiscuously pollinated by various kinds of bees. In the western hemisphere there are *Sobralia*, *Vanilla*, *Bletia* and possibly many of the lower *Epidendrinae*. In the eastern hemisphere similar orchids are *Phajus*, *Dendrobium*, *Bletilla*, *Coelogyne* and *Thunia*.

Pseudocopulation has been extensively reported in the genus *Ophrys* in Euroupe and in *Cryptostylus* in Australia. Though such phenomena have not been reported in the western hemisphere a number of orchids have characteristics which indicate that such will be reported in the future.

Glossary of Unfamiliar Terms Used in This Paper

Antenna; pl. **antennae.** A slender appendage on each side of the column of *Catasetum*; the "trigger" which sets off the pollen-throwing mechanism.

Column. The central portion of the orchid flower, which is formed by the partial or complete union of the male and female parts (stamens and style).

Femur. The third segment of an insect's leg (counting from the base), situated between the trochanter and the tibia.

Frons. The facial area of an insect's head.

Hypochile. The basal portion of the lip in *Stanhopea* and related genera.

Metathorax. The posterior division of an insect's thorax.

Pollinarium. The complete set of pollinia with associated parts—viscidium or viscidium and stipe.

Pollinium; pl. **pollinia.** In the orchids, a more or less compact mass of pollen.

Proboscis. An elongate but not rigid (often curled) feeding organ of certain insects, such as flies and butterflies, which is of the mouth parts.

Resupinate. Having the pedicel of the flower twisted so that the part of the flower which is uppermost in bud (the lip) is on the lower side when the flower matures.

Rostellum. A portion of the stigma which is specialized to take part in the pollen transfer from one flower to another; the tissue which separates the anther and the functional stigma.

Stipe. A non-viscid band or strap of columnar tissue which connects the pollinia to the viscidium, as in *Oncidium* and *Vanda*.

Tarsus. The fifth segment of an insect's leg.

Thorax. The portion of the body of an insect located between the head and the abdomen.

Tibia. The fourth segment of the leg, between the femur and tarsus, analogous to the shin bone.

Trochanter. The first segment of the leg of an insect, to which the femur is attached

Viscidium. A viscid part of the rostellum which is removed with the pollinia as a unit, and serves to attach the pollinia to an insect.

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SOME FACTS ABOUT SHAW'S GARDEN

The Missouri Botanical (Shaw's) Garden was established in 1859 by Henry Shaw, a St. Louis businessman, to be controlled by a Board of Trustees for the public benefit. The Garden is a non-profit institution which receives no support from the city or state, depending on the income from the Shaw estate supplemented by contributions from the public.

The old stone walls and cast-iron fences, the Linnean House, the Museum Building, the part of the Administration Building which was Shaw's Town House, relocated in the Garden in 1890, and the Tower Grove House, his country home, all date from Mr. Shaw's time. The Main Gate, display and growing greenhouses and most other facilities date from the period immediately following the turn of the century. The Climatron, opened in 1960, is the first of several new buildings planned for the Garden's redevelopment. It is the world's first geodesic dome, fully climate-controlled greenhouse and contains the Garden's tropical collections.

The Garden—70 acres—is open every day of the year from 9:00 A. M. until sundown; the greenhouses 9:00 A. M. to 5:00 P. M.; the Climatron Monday through Thursday 9:00 A. M. to 6:00 P. M., Friday through Sunday 9:00 A. M. to 10:00 P. M. (April through October); Tower Grove House is open daily from 12:00 M. to 4:00 P. M. (December to March on weekends only). The Display House presents four seasonal displays: November, Chrysanthemums; December, Poinsettias; February, Orchids; Spring, Lilies and other flowers. During the year are other shows, competitions and festivals sponsored by various Garden Clubs and Flower Societies.

Courses in Botany and Horticulture for adults are conducted by the Garden staff. Children's nature studies are provided each Saturday of the year and a special nature program is held during the summer. Information on these activities is published in the BULLETIN or may be had by mail or phone. The Garden maintains a research program through the Henry Shaw School of Botany, Washington University.

In 1926 an Arboretum — 1600 acres — was established at Gray Summit, Missouri. Foot trails and roads pass through the Arboretum and are open to visitors in April and May.

The Garden Administration Building is located at 2315 Tower Grove Ave., and the Garden main entrance is at Tower Grove and Flora Place. The entrance at Tower Grove and Cleveland Avenue is also open to the public. The Garden is served by both the Sarah (No. 42) and the Park-Southampton (No. 80) city bus lines.

Persons interested in helping to support the Garden and taking part in Garden activities are urged to do so through the "Friends of the Garden". Information may be obtained from the Main Gate or by mail or phone.